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Contact rates with nesting birds before and after invasive snake removal: estimating the effects of trap-based control

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Abstract

Invasive predators are responsible for almost 60% of all vertebrate extinctions worldwide with the most vulnerable faunas occurring on islands. The brown treesnake (*Boiga irregularis*) is a notorious invasive predator that caused the extirpation or extinction of most native forest birds on Guam. The success of avian reintroduction efforts on Guam will depend on whether snake-control techniques sufficiently reduce contact rates between brown treesnakes and reintroduced birds. Mouse-lure traps can successfully reduce brown treesnake populations at local scales. Over a 22-week period both with and without active snake removal, we evaluated snake-trap contact rates for mouse- and bird-lure traps. Bird-lure traps served as a proxy for reintroduced nesting birds. Overall, mouse-lure traps caught more snakes per trap night than did bird-lure traps. However, cameras revealed that bird-lure traps had a snake contact rate almost 15 times greater than the number of successfully captured snakes. Snakes that entered bird-lure traps tended to be larger and in better body condition and were mostly captured in bird-lure traps, despite numerous adjacent mouse-lure traps. Traps placed along grid edges caught more snakes than interior traps, suggesting continuous immigration into the trapping grid within which bird-lure traps were located. Contact between snakes and bird-lure traps was equivalent before and after snake removal, suggesting mouse-lure traps did not adequately reduce the density of snakes that posed a risk to birds, at least at the timescale of

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this project. This study provides evidence that some snakes exhibit prey selectivity for live birds over live mouse lures. Reliance on a single control tool and lure may be inadequate for support of avian reintroductions and could lead to unintended harvest-driven trait changes of this invasive predator.

Keywords
Avian recovery, biological invasions, brown treesnakes, control, Guam, restoration

Introduction

Invasive predators are a major driver of vertebrate extinctions globally (Szabo et al. 2012; Doherty et al. 2016). Although mammalian predators are the primary cause (Doherty et al. 2015), invasive snakes have also been linked to extinctions and extirpations of native vertebrates (Savidge 1987; Dorcas et al. 2012). Reducing or eradicating invasive predators can lead to recolonization of nesting sites (Borrelle et al. 2016), increased prey populations (Campbell et al. 2012), and recovery of native species (Jones et al. 2016). In a systematic worldwide review, predation by non-native predators was identified as one of the leading drivers for failed reintroductions (Destro et al. 2018), where reintroduction is defined as a type of conservation translocation that entails deliberate releases of individuals within their native range where they have otherwise been extirpated (IUCN/SSC 2013). For native species that have been locally extirpated or driven to extinction in the wild in part by predation by invasive predators, removal or reduction of non-native predators is essential (Choquenot and Parkes 2001; VanderWerf et al. 2014). Therefore, when invasive predators are present, management and suppression of their populations is often a component of native species recovery plans (U.S. Fish and Wildlife Service 2006; IUCN/SSC 2013) and may be critical when recovery of native species requires reintroduction efforts (Côté and Sutherland 1997; Smith et al. 2010).

In regions where biodiversity is affected by invasive predators, core components of invasive predator control include exclusion, shooting, trapping, and toxicant baiting (O'Donnell et al. 2017). Because species recovery is often linked to predator control, assessing the impact of such programs on the anticipated interactions between non-native predators and the species targeted for recovery is crucial for population restoration (Choquenot et al. 2001). Prioritizing these evaluations during pre-release planning or post-release monitoring may increase the success of reintroduction programs (Destro et al. 2018), encourage adaptive management, and allow refinement of control tools and lures (Klug et al. 2015).

Guam, the southernmost island in the Mariana Archipelago, experienced major biodiversity loss after the introduction of the non-native brown treesnake, *Boiga irregularis*, after World War II (Savidge 1987; Wiles et al. 2003). This accidental introduction resulted in high snake densities across the island and caused the extirpation of many native terrestrial vertebrates, with 10 of 12 forest bird species eliminated (Savidge 1987; Wiles et al. 2003; Rodda and Savidge 2007). Declines and reductions of bird populations on Guam are suspected to be causing major ecological changes to

forest structure and composition (Rogers et al. 2017). Therefore, reintroducing, reinforcing, and otherwise recovering native bird populations on Guam are considered a critical goal for broader restoration targets. Suppression and removal of invasive brown treesnakes are a critical management need for recovery of Guam's native birds.

Localized brown treesnake control on Guam to reduce snakes at seaports, airports, and caves used by Mariana swiftlets (*Aerodramus bartschi*) has historically relied on removal primarily using mouse-lure traps (Rodda et al. 1999; Clark et al. 2018) but experimental aerial application of toxicant baits (dead neonatal mouse with acetaminophen tablet) to suppress snake populations is emerging as a potential landscape-scale control tool (Dorr et al. 2016; Siers et al. 2019). Mouse-lure traps can remove every individual of suitable size (≥950 mm snout-vent length) at a small spatial scale, given intensive effort (Tyrrell et al. 2009). The effect of extensive snake trapping on predation rates on birds (and therefore the likelihood of successful bird restoration efforts) has not been quantified. We therefore evaluated the potential benefits of trap-based snake removal for bird reintroductions by simulating the avian nesting period because that aspect of the life-cycle is vulnerable for birds (Martin 1993; Yackel Adams et al. 2006). Specifically, we 1) measured the fraction of trap contacts that resulted in a snake capture, 2) compared brown treesnake contact rates between mouse- or bird-lure traps, and 3) compared contact rates between bird-lure traps (used as a proxy for reintroduced nesting birds) and brown treesnakes before and after active snake control (trapping with mouse lures). The results are interpreted in the context of brown treesnake management to understand the actual complexities inherent to reintroductions or reinforcements of native bird populations on Guam.

Methods

Study site

The study occurred in the Ritidian Unit of the Guam National Wildlife Refuge (GNWR; 13°39'N, 144°51'E), at the northernmost tip of Guam. The 155 ha terrestrial portion of the refuge consists of coastal strand forest interspersed with degraded areas that have been colonized by non-native shrubs and trees (U.S. Fish and Wildlife Service 2009). The site is bordered to the south by limestone cliffs and to the north by the Pacific Ocean. In 2012, a multi-species barrier fence was constructed around 51 ha of the Ritidian Unit; this fence included a one-way barrier designed to exclude snakes while allowing snakes on the refuge to leave the enclosed area (Rodda et al. 2007). Snake control efforts were implemented in 2013 through use of mouse-lure snake traps (15,447 trap nights that removed 392 snakes) to suppress brown treesnakes within the barrier at the GNWR. Based on that control effort, GNWR was considered a snake-suppressed area (Nafus et al. 2018) and was used to measure contact rates between birds and brown treesnakes. Snake density within the barrier was unknown at the time of the 2013 removal effort, but 23 snakes per hectare has been documented in a nearby

enclosed forested habitat (Christy et al. 2010). If we assume that density estimate along with the assumption that every hectare within the refuge barrier is suitable snake habitat, then we have a snake population of 1,173 (23 snakes/ha × 51 ha). This rough estimate indicates that one-third of the snake population may have been removed during the 2013 removal effort. Although the snake barrier had by 2014 partially degraded (i.e., small patches of rusted fencing due to salt spray) and probably allowed some immigration, the barrier was mostly intact and abutted a road. Brown treesnakes avoid crossing roads (Siers et al. 2016) and thus the road may have hindered snake crossing into GNWR, improving the efficacy of the barrier. Limited and sporadic rat and feral pig control measures were implemented within the barrier.

Trapping array and capture rates

In May 2014, we established a 6 × 18 trapping grid (510 m × 150 m; Fig. 1a) of 108 live mouse-lure traps (Fig. 1a [yellow dots] and Fig.1b) with 16 live bird-lure traps (Fig. 1a [red and blue dots] and Fig. 1c). We used Japanese quail (*Coturnix japonica*) in place of a native bird species. Japanese quail are neither present in the wild on Guam nor a federally/territorially listed species, but likely functionally equivalent to Guam rail (*Gallirallus owstoni*) in terms of prey odor and habitat strata use. Bird-lure traps thus served as a proxy for a reintroduced population of nesting birds and were set 2 weeks prior to the mouse-lure traps (Phase I) to obtain baseline predation rates in the absence of active snake control (Phases I and II). After 2 weeks, we added mouse-lure traps, but continued to trap without removing snakes for 60 days (Phase II). Beginning on 07 July 2014 (day 61) we removed all snakes captured in mouse-lure traps to monitor contact rates during active suppression efforts (Phase III). Snakes trapped in bird-lure traps were, however, never removed to simulate realistic snake contacts with nesting birds.

Mouse-lure and bird-lure traps are modified commercial minnow traps composed of 6 mm galvanized steel mesh (Rodda et al. 1999; Fig. 1b, c). Each mouse-lure trap contained a lure chamber and PVC pipe refuge for trapped snakes. Lure chambers were constructed of galvanized steel mesh and held a single mouse (20–40 g) that was provided a grain mixture embedded in paraffin and a piece of raw potato for water. Bird-lure traps were modified versions of the commercial minnow trap, with a central extension to provide room for the birds (Fig. 1c). Bird chambers (35 × 13 × 17 cm, LWH) inside the traps were constructed of galvanized steel mesh (6 mm). Birds (150–180 g) were provided a pellet seed mixture, millet sprig, and water. Both trap types allowed multiple snake captures. Bird-lure traps were checked daily and mouse-lure traps checked every other day. Mouse-lure traps were stationary during the study (to mimic operational control efforts) whereas the two lines of bird-lure traps moved weekly to the next available grid space, to sample a larger percentage of the grid. For instance, bird-lure traps in week 1 (configuration shown in Fig. 1a) deployed between the transect lines of D and E, and B and C would move north (toward the ocean) one grid space in week 2 to occupy grid locations between C and D and A and B, respectively.

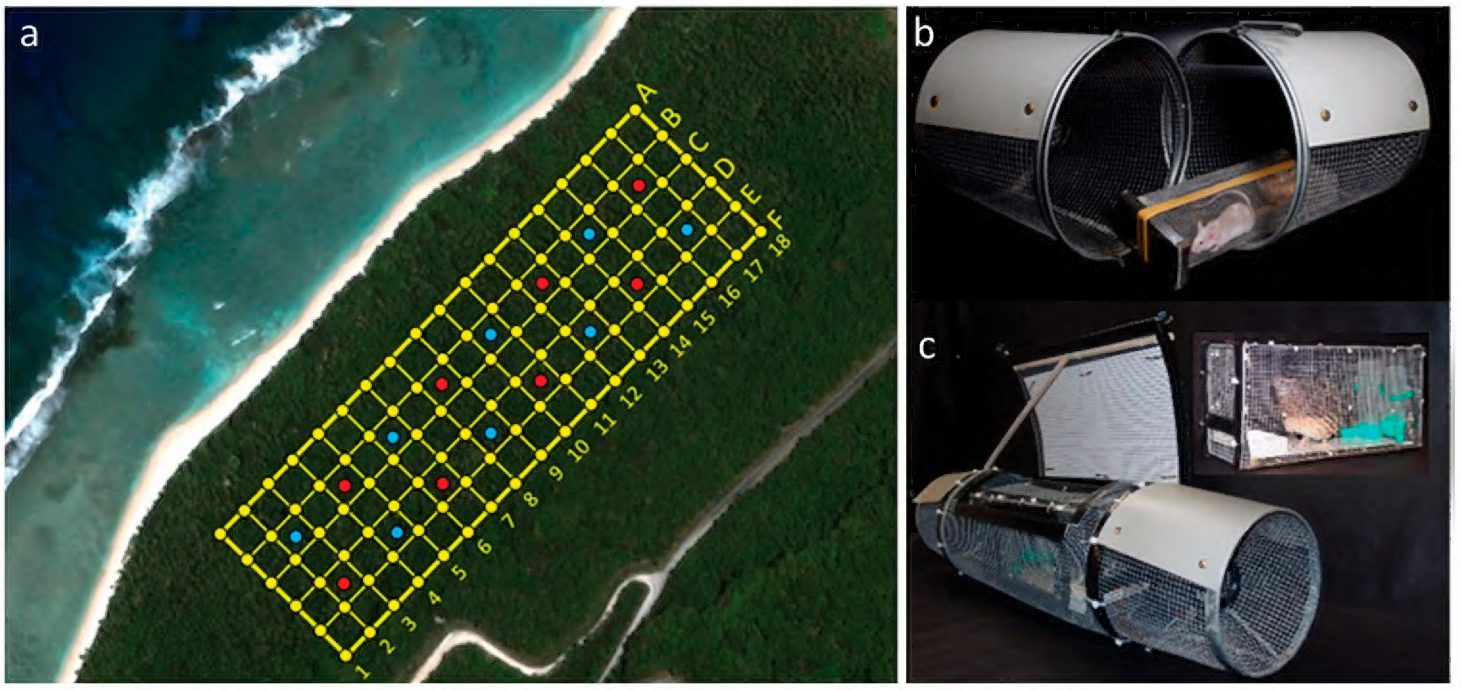

Figure 1. The 7.65 ha grid consisted of 124 traps (**a**). Yellow dots represent mouse-lure traps (n = 108 traps) whereas red and blue dots represent bird-lure Japanese quail (*Coturnix japonica*) traps (n = 16) with and without cameras, respectively. Mouse-lure traps (**b**) were spaced every 30 meters and were stationary. Bird-lure traps (**c**) were spaced at 60 meters and were moved weekly to a new location. For instance, bird-lure traps in week 1 (configuration as shown in **a**) would move in week 2 from the alpha transect lines of BC and DE to AB and CD, respectively. New locations would remain in the same numeric transect lines of 2–3, 4–5, 6–7, 8–9, 10–11, 12–13, 14–15, and 16–17 (until all interior spaces had been sampled) before shifting in week 6 to numeric lines of 3–4, 5–6, 7–8, 9–10, 11–12, 13–14, 15–16, and 17–18. Each bird-lure trap location was sampled two times for a total of two weeks. The snake barrier fence runs along curved road line (bottom right of panel a). Photo credit for 1b: Shane R. Siers.

To quantify the proportion of snake-bird contacts that failed to result in trap captures, eight of the bird-lure traps were fitted with trail cameras at a 1.8 m focal distance (Reconyx PC 900 HyperFire Professional covert camera; Fig. 1a [red dots]). We programmed cameras with both time-lapse (30-sec intervals between the hours 1800 and 0600 [brown treesnakes are nocturnal; see Suppl. material 1 for example camera images]) and motion sensor modes (any time of day). Cameras were placed 1.8 m from the focal trap and batteries and SD memory cards were changed every 3 days. Digital images were downloaded and transcribed to record all snakes visible in the camera field of view (FOV) as well as other potential predators. Brief absence from FOV, return to FOV in close spatial proximity to FOV departure location, similar physical attributes [broken tail, size] were counted as a single snake. Trap contact consisted of the snake making physical contact with the trap.

Snake morphometrics

Unless destined for removal (during Phase III), we marked trapped snakes on the first occasion we encountered them, before re-releasing them at the site of capture. Marking consisted of a passive integrated transponder (PIT) tag injected intraperitoneally,

and a unique series of ventral scale clips. Measurements of mass and snout-vent length (SVL) were recorded for each snake capture. Individual body condition was calculated as the ratio of mass to its expected mass given its length. Expected mass for a given SVL was estimated by linear regression on logarithmic scales, based on >10,000 records of brown treesnakes. Snakes that we removed (Phase III: active control, mouse-lure traps) were euthanized using procedures approved by the American Veterinary Medical Association (2013) and USGS Fort Collins Science Center, Institutional Animal Care and Use Committee (FORT IACUC 2013-13).

Statistical analyses

We used Poisson regression to test the effect of lure type (bird or mouse) on catch per unit effort (CPUE) during Phase II of the project when both bird- and mouse-lure traps were present on the landscape, but snake removal was not occurring. CPUE was measured as the number of snakes captured per 100 trap nights, where a trap night is defined as 1 trap active for 1 night. We used multivariate multiple regression to measure the effect of trap lure type and time since project initiation on SVL and body condition. We included both SVL and body condition as dependent variables in the model. Although we were primarily testing for the effect of bird-lure versus mouse-lure traps as a predictor of SVL and body condition, we included time (days) since project initiation as a covariate due to changes in snake population structure that can result from active removal or seasonal effects. We used Pearson's chi-square to test for a change in contact rates between snakes and bird-lure traps or cameras after the onset of snake removal. For the chi-square we compared camera and trap CPUE (snakes per 100 days of trapping) prior to active removal to CPUE after trap-based removal began. Finally, we used mixed-effect, zero-inflated Poisson regression (GLMMADMB package in R) to test for differences in snake capture rates between mouse-lure traps near a bird-lure trap and those not near one, as well as for differences between grid edge versus interior mouse-lure traps. We included alpha trap transect lines (A–F; Fig. 1a) as a random effect to account for repeated measures and spatial variation in trap captures. In Figure 1a, all grid interior mouse-lure traps were considered adjacent to a bird-lure trap and all grid edge traps as non-adjacent. Interior and edge classification would change weekly as the bird-trap deployment was altered by weekly trap placement (defined above). All analyses were executed in program R (R Core Team 2017) and descriptive statistics reported as mean ± SE.

Results

Over the course of the study (08 May to 05 Oct. 2014), we recorded 159 unique snakes from 227 captures during 16,947 trap nights (0.013 snakes/trap night). Fe-

males (n = 82) averaged 1035 mm SVL (range 688–1,265; body condition = 1.15, range 0.82–1.54). Males (n = 77) averaged 1081 mm SVL (range 773–1,400; body condition= 1.07, range 0.71–1.39). Of the 227 captures, 198 snakes were captured in mouse-lure traps (134 individuals; 0.014 snakes/trap night) and 29 were captured in bird-lure traps (25 individuals; 0.012 snakes/trap night).

Camera and trap CPUE

In order of prevalence, surveillance cameras deployed on eight bird-lure traps captured 2,314 FOV incidents from feral pigs (1,727), snakes (307), rats (228), monitor lizards (44), and cats (8). Of the 307 FOV records for snakes, 217 snake encounters were considered independent snakes for that evening. Fifty-six percent (122 of 217) of the images revealed a trap contact by the snake, suggesting interest in the bird lure. Overall snake CPUE at camera traps was 0.18 (Fig. 2), yielding a contact rate of 18 snakes/100 camera-trap nights. However, only 13% of trap contacts resulted in a trap capture (Fig. 3). Cumulatively, bird-lure traps captured 29 snakes across 2,321 total trap nights (1.2/100 bird-lure trap nights). Thus, trap captures underestimated the trap-contact rates with birds 15-fold relative to trap-contact rates estimated by camera traps. Snakes that successfully entered the bird-lure traps spent on average 55 min to enter (8 min up to 2 hours and 23 min). Snakes that failed to gain entry to the trap gave up and departed the FOV on average after 17 min (30 s to 50 min).

Snake contact rates with bird- and mouse-lure traps

During Phase II, when both bird- and mouse-lure traps were deployed but no active snake removal occurred, we recorded 732 bird-lure trap nights and 4,942 mouse-lure trap nights. Bird-lure traps captured six snakes (0.8 snakes/100 bird-lure trap nights) and mouse-lure traps captured 69 snakes (1.4 snakes/100 mouse-lure trap nights). A small portion of snakes (14%) were repeatedly captured in mouse-lure traps (≥ 2 times) and almost all unique captures during Phase II were snakes only captured in mouse-lure traps (95%). Mouse-lure traps had a CPUE that was 1.7 times greater than bird-lure traps based on Poisson regression (z = 4.1, $P < 0.001$, 95% Confidence Interval [CI] = 0.29, 0.82, Fig. 2).

The 25 unique snakes captured in bird-lure traps averaged 26 mm longer and 19 g heavier than snakes captured in mouse-lure traps (Table 1). Mean body condition for snakes captured in bird-lure traps was 1.16 ± 0.03 and 1.12 ± 0.01 for mouse-lure traps (Table 1). Multivariate multiple regression indicated a weak negative relationship between mouse-lure traps and SVL and body condition of snakes captured (t = –2.0, P = 0.04, 95% CI = –0.186, –0.002) and a negative effect of time since project initiation (t = –2.2, P = 0.02, 95% CI = –0.0016, –0.0001). Although

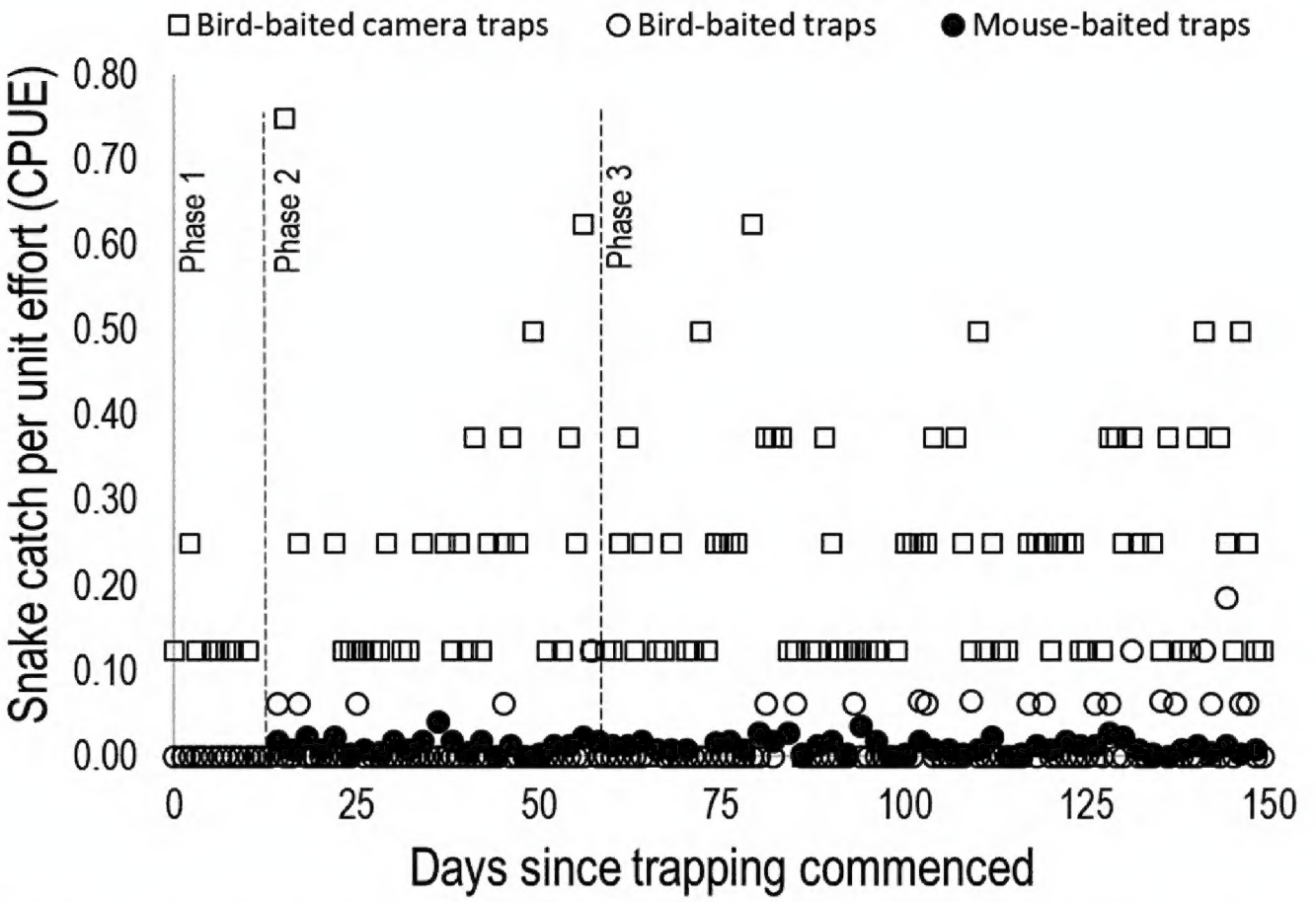

Figure 2. Brown treesnake catch per unit effort (CPUE) per trap night for bird-lure camera traps and bird- and mouse-lure live traps from 08 May through 05 October 2014 on the Guam National Wildlife Refuge, Guam. Open squares represent capturing a photographic image of the snake. Open and closed circles represent actual successful snake captures from traps. Phase I = only bird-lure traps deployed, Phase II = both bird- and mouse-lure traps deployed, and Phase III = both bird- and mouse-lure traps deployed with snake removal from mouse-lure traps only. Cameras were deployed on bird-lure traps during all three phases.

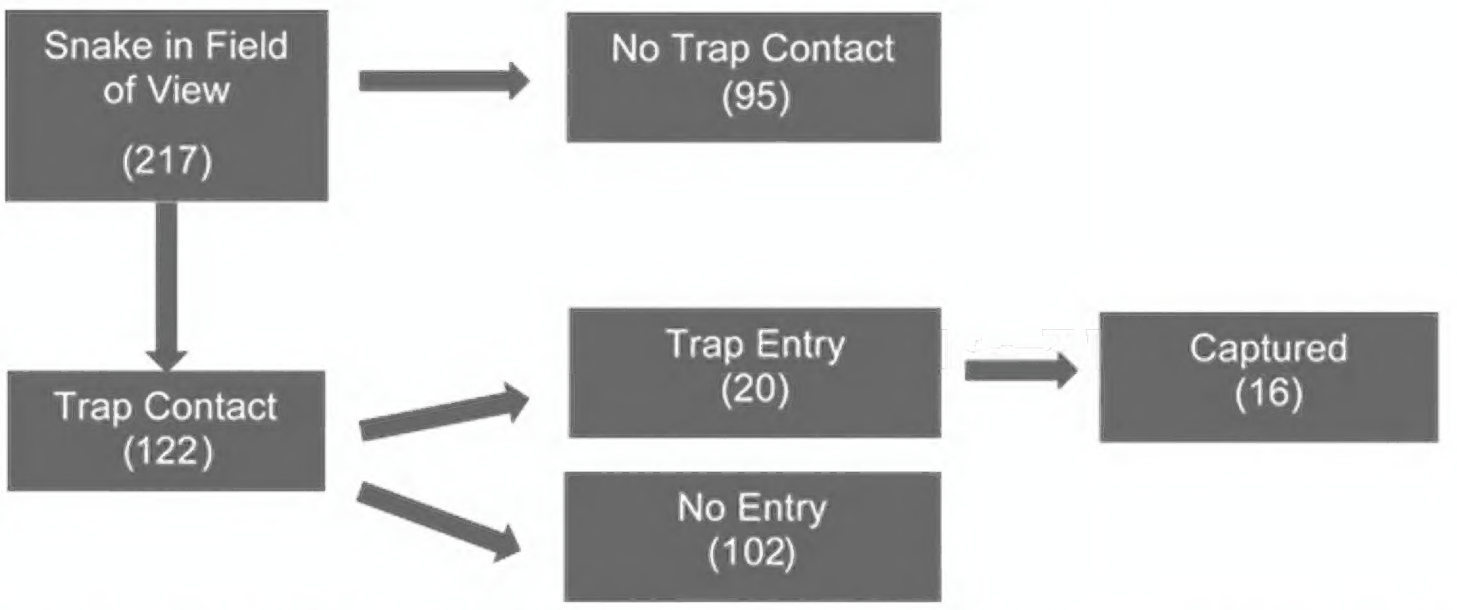

Figure 3. Schematic of brown treesnake activity outcomes at bird-lure camera traps (n = 8). A portion of snake observations were probably repeated instances of one snake's efforts to capture the prey (e.g., brief absence and return to field of view in close spatial proximity to departure location and similar physical attributes [broken tail, size]) and were therefore counted as a single snake event. Trap contact consisted of the snake making physical contact with the trap. Trap entry consisted of snakes using either entrance to enter the trap. Values listed parenthetically represent the number of snakes for a specified outcome, with snakes captured in traps being the desired outcome for management.

Table 1. Morphometrics of individual brown treesnakes (*Boiga irregularis*) trapped with live mouse- and/or live bird-lures based on first encounter presented as mean ± SE (range), Guam National Wildlife Refuge 2014.

Lure	BC[1]	BC range	SVL (mm)	SVL range (mm)	Mass (g)	SVL>1150 (mm)
Bird-lure n = 25	1.2	0.89–1.46	1091	885–1304	160 (60–352)	35%
Mouse-lure n = 140	1.1	0.71–1.66	1065	688–1400	141(29–435)	25%

[1] Body condition (a value of < 1 represent relatively underweight individuals, average condition snakes = 1, and higher than average are > 1).

some individuals were repeatedly captured in bird-lure traps, 20 of the 25 unique bird-lure captures (80%) were only captured in bird-lure traps. Three individuals (12%) were captured more than once in bird-lure traps, but never in mouse-lure traps. Five individuals were captured in both trap types and were removed during Phase III, suggesting 20% of snakes that entered a bird-lure trap were effectively removed by mouse-lure trapping.

Contact rates with traps pre- and post-removal

During Phase III, we removed 128 snakes from the trap grid using mouse-lure traps. Despite removal, overall daily CPUE of snakes in mouse-lure traps remained constant but low (1.4 snakes/100 mouse-lure trap-nights). Camera trap CPUE at bird-lure traps prior to snake removal (Phases I and II) was 14 snakes/100 camera-trap nights and 19 snakes/100 camera-trap nights after snake removal began. Trap CPUE for bird-lure traps was 0.6 snakes/100 bird-lure trap nights prior to snake removal and 1.7 snakes/100 bird-lure trap nights after snake removal began (translating to 1.3 snakes/100 bird-lure trap nights overall). There was no significant effect of snake removal and snake contact with birds (χ [1] = 0.20, P = 0.65) in Phase III as compared to Phases I and II. Overall, the number of consecutive days without a capture (n = 29 snakes) in a bird-lure trap decreased over time despite snake removal and weekly movement of bird-lure traps from 10.4 days during the first 5-week interval to 1.6 days during the last 5-week interval (Fig. 4a).

There were also spatial effects on snake captures independent of snake removal. Almost half of the 29 bird-lure captures occurred between trap lines E and F (Fig. 1a), and mouse-lure captures on line F also had the highest CPUE (Fig. 4b). Although mouse-lure traps did not appear to suppress bird-trap contact rates, they did suppress contact rates with mouse-lure traps. Mixed-effect Poisson regression indicated approximately 50% fewer snakes were captured in traps deployed in the grid interior relative to edge traps (β = –0.67, SE = 0.21, P = 0.002). Across 20 weeks of mouse-lure trapping, grid edge traps captured 80 snakes (44 edge traps), compared to 60 snakes captured in interior traps (64 interior traps). Mouse-lures near bird-lures, however, had the same CPUE as those that did not have a bird-lure present (β = –0.10, SE = 0.21, P = 0.65). Therefore, captures of snakes attracted to mouse lures were depressed in the grid interior but there was no evidence for a similar effect for bird lures.

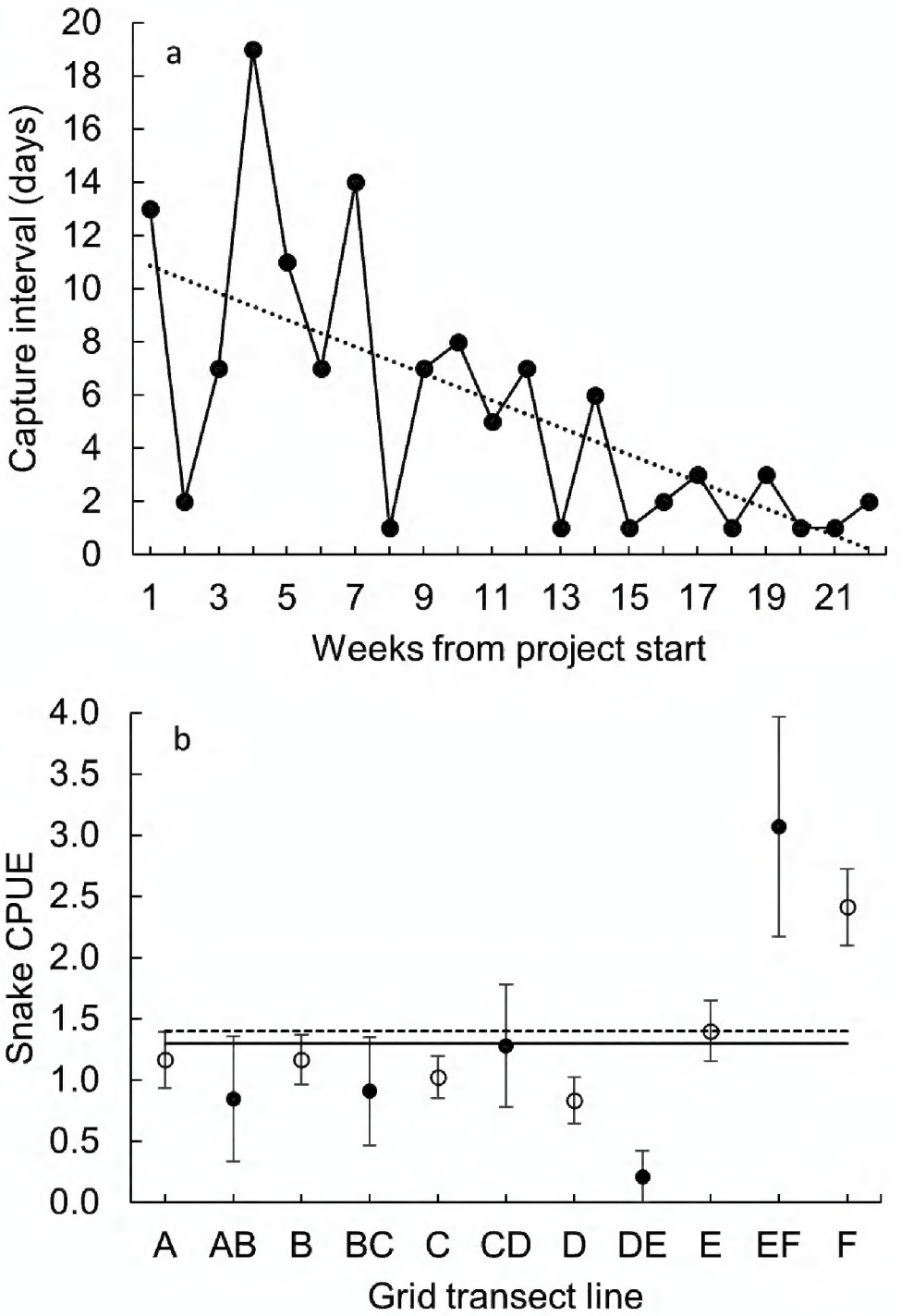

Figure 4. We observed temporal (**a**) and spatial (**b**) effects on brown treesnake captures at bird- and mouse-lure traps (note: graphs do not include camera data). Capture intervals (days between capturing any snake in a bird-lure trap) decreased as length of time from study start date increased (**a**). Catch per unit effort (CPUE, snakes/100 trap nights) was greater for bird-lure (closed circles) and mouse-lure (open circles) transects that were closer to the cliff-line (E–F; see **b**). In panel b, the solid black line indicates mean bird-lure trap CPUE and dashed line is mean mouse-lure trap CPUE from this study.

Discussion

Traps with live bird lures had a contact rate with snakes that was almost 15 times greater than the number of snakes that were successfully captured. Unpublished data from cameras referred to in Clark et al. (2012) and visual observations using night-vision goggles (G. Rodda, personal communication) at mouse-lure traps also showed that most snakes that tried to enter the traps failed to do so. Such collective evidence suggest that such trapping failures are common and that some snake individuals may

be more difficult to trap. Despite the fact that 87% of our bird-lure traps failed to capture a snake, prior research in a 5 ha enclosed area of snakes has shown that all snakes of trappable size can be trapped in mouse-lure traps given intensive trapping over time (Tyrrell et al. 2009). Brown treesnakes begin to prey on birds around 750–950 mm SVL (Siers 2015), similar to the size at which they become trappable using live mouse lures (Tyrrell et al. 2009); of 555 snakes from various habitats with prey in their stomachs, the smallest BTS to contain an avian prey item (domestic fowl chick) was 717 mm SVL (Siers pers. comm.). Thus, with intensive effort, mouse-lure traps can target individual snakes large enough to consume birds. However, our results suggest that a trapping effort that is less than landscape-scale saturation (e.g., our trapping grid of 7.65 ha out of 51 ha behind a barrier) removed only 20% of snakes that entered a bird-lure trap and did not suppress snakes enough to reduce contact rates with birds.

Savidge (1991) noted that mouse-lure traps along the edge of a trapping grid captured more brown treesnakes than did traps deployed in interior portions of the grid. The difference in captures between our edge and interior traps was at least partially explained by high captures rates on the transect line (F) parallel to a small cliff-line ridge and abundant habitat. The overall increase in the number of brown treesnakes captured in traps placed at the edge of the grid suggests brown treesnake depletion was not occurring at least in part due to continued immigration into the trapping grid. Effective barriers (Rodda et al. 2007) adjacent to control areas can eliminate snake immigration (Tyrrell et al. 2009; Christy et al. 2010), but our trapping grid was not immediately adjacent to the snake-proof barrier. Snake density associated with the trapping grid is unknown, so we are unable to determine if reduced interior contact rates for mouse-lure traps resulted from an overall reduction in brown treesnakes or reduced interest in mouse-lure traps from those snakes that remained. The fact that shifting bird-lure traps had equivalent contact rates prior to snake removal as they did afterwards indicates that the stationary mouse-lure traps did not adequately reduce the density of snakes interested in birds.

Even though the landscape around the bird-lure traps had a high density of mouse-lure traps, most (68%) of the snakes that were captured in bird-lure traps were not recaptured in either bird- or mouse-lure traps. Mouse-lure traps, however, captured more snakes per unit effort than bird-lure traps, a finding documented in another study at the GNWR (Klug et al. 2015). Mice may produce a generally more attractive or stronger odor plume than birds (Rodda et al. 1999). Alternatively, the strong edge effect on trap capture success combined with the fact that bird-lure traps were always deployed in the grid interior may have partially driven the different capture success documented in this study. Additionally, snakes that entered bird-lure traps tended to be larger and in better body condition. Quail (150–180 g) are much larger than mice (20–40 g) and if brown treesnake size partially drives prey preference (Savidge 1988), then quail may be attractive to slightly larger snakes. Overall, large snakes are less common on Guam except in urban locations (Savidge 1991; Siers et al. 2017) and thus there may be few snakes on GNWR that are large enough to be attracted to quail.

While quail may be too large for many snakes, mice should still be of interest to larger snakes, as rodents are an important component of the diet of snakes >800 mm SVL on Guam (Savidge 1988; Siers 2015). Despite this, only 20% of all snakes captured in bird-lure traps were ever captured in stationary mouse-lure traps, despite the abundance of nearby mouse-lure traps in Phases II and III. The recapture rate for brown treesnakes captured in a bird-lure trap was 32% overall, which suggests that these snakes did not fully avoid traps. Whether a morphological- or individual-based preference, our observation that some snakes were willing to enter a trap with a bird but not a mouse lure provides limited evidence that snakes may vary in their dietary preferences. Many animals have been documented to specialize on a small subset of the dietary breadth of their species (Bolnick et al. 2002a, 2002b). We do not think that the stationary nature of mouse-lure traps combined with the weekly shifting of bird-lure locations is problematic for our interpretations because we maintained both spatial and temporal balance of traps and lure types throughout our study period.

Populations can experience trait changes in response to harvesting pressure (Palkovacs et al. 2018). Invasive species control measures resulting in non-random removal of individuals from targeted populations can lead to population-level shifts in mean trait values (Zavorka et al. 2018). Selection that reduces control tool efficacy within a population can be minimized by implementing multiple tools/lures to remove individuals from the population, in hopes that different tools will target individuals with distinct trait values (Palkovacs et al. 2018). Therefore, multi-faceted control techniques that include alternate lure forms or distinct treatments occurring concurrently may improve the overall outcome of brown treesnake control to support bird recovery (as can multi-faceted control efforts for invasive rats; Russell et al. 2008).

Beyond the benefits of reducing individuals resistant to capture, a multi-faceted control approach is expected to improve efficacy for other reasons. For example, camera trap imagery demonstrated that snakes were highly motivated to contact birds, with one snake spending over 2 hours attempting to access the bird. To enter a trap, however, snakes must find the trap entrance. Thus, control techniques that require less problem-solving by the snakes (e.g., open-ended bait tubes) (Lardner et al. 2013; Clark et al. 2018) may increase the odds of successful bird reintroductions via enhanced snake control. Brown treesnakes have been dramatically suppressed in experimental test plots by aerial delivery of dead neonatal mouse baits treated with 80 mg of acetaminophen (Dorr et al. 2016; Siers et al. 2019). Use of live-lure trapping and aerial delivery of toxicants may target a higher proportion of the snake population by targeting snakes attracted to rodents but unable to easily solve the problem of how to enter a trap. In contrast, individuals that are attracted to live prey over carrion may be more effectively targeted by traps with live lures. There is some evidence that carrion is less attractive to very large brown treesnakes (Shivik et al. 1999) and thus live-lure traps may be an essential component for targeting the largest individuals in a population.

Remote cameras aimed at bird-lures reliably captured nocturnal brown treesnake presence and behavior but required the use of high frequency photography (30-second intervals) because snakes failed to trigger the infrared sensors. Of the other potential nest predators detected (feral pigs, rats, monitor lizards, and cats), the high nocturnal

sighting rates of feral pigs (1.43 pigs/camera trap night) would be problematic for reintroduced ground-nesting birds (e.g., Guam rail; *Gallirallus owstoni*). Cameras in association with avian lures may have a promising role in assessing predation risk or may act as a sentinel for detecting snake ingress into previously snake-eradicated areas. We recognize that all successful lures used in snake control to date rely on a food attractant (Rodda et al. 1999) and that snake suppression will allow recovery of prey populations, thus depressing future snake detection via food-based lures. That said, we documented that 44% of the snakes viewed on cameras failed to physically interact with the trap and its lure (Fig. 3).

The average interval between snake captures in bird-lure traps also decreased with time (from 10.4 days during the first 5-week interval to 1.6 days during the last 5-week interval), suggesting that the longer traps were on the landscape the more frequently they were visited by snakes. Odor cues from the traps may have accumulated, attracting snakes from greater distances. It is also possible that snakes were drawn in gradually at a constant rate (either from the scent or random movements in the landscape), without any increase in the grid's attraction rate, and that bird-attracted snakes (not removed by mouse-traps in Phase III) simply became increasingly common as they decided to move no further but to stay near birds. Alternatively, the study progressed in time through the wet season and trapping during the wet season has been shown to result in higher CPUE (Nafus et al. 2018).

Conclusions

Snake trapping around a small-scale simulated bird reintroduction site (bird-lure traps) did not demonstrably reduce brown treesnake contact rates with birds as compared to trap-contact rates prior to initiating snake removal in a snake-suppressed landscape. Trapping efforts required to meaningfully suppress brown treesnakes in support of bird recovery over large areas of Guam are assumed to be cost-prohibitive. Integration of new technologies such as the aerial delivery of toxicants is likely to be required to sufficiently suppress snakes at spatial scales large enough to support bird restoration efforts. However, this study provides evidence that some snakes may select live birds over live mouse lures, and thus reliance on a single control tool and lure may be inadequate for support of avian reintroductions and could lead to unintended harvest-driven trait changes within snake populations. Integration of multiple control tools and multiple lures is thus thought to yield the best management outcomes for reintroduction and recovery of native vertebrate species on Guam.

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Supplementary material 1

Select camera images of a failed brown treesnake (Boiga irregularis) trap capture using a bird lure

Authors: Amy A. Yackel Adams

Data type: TIF File (.tif)

Explanation note: Select time-lapse camera photos (4 images) of a failed capture at a bird-lure trap by a single brown treesnake. This individual attempted to secure the bait for 35 minutes and 30 seconds before leaving the trap area. White arrows point to the eye shine of the snake. Overall, camera traps revealed a much higher snake contact rate with bird lures than did bird-lure live trap data alone.

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